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NOTES ON THE ANATOMY OF PERIDERMIUM GALLS. I

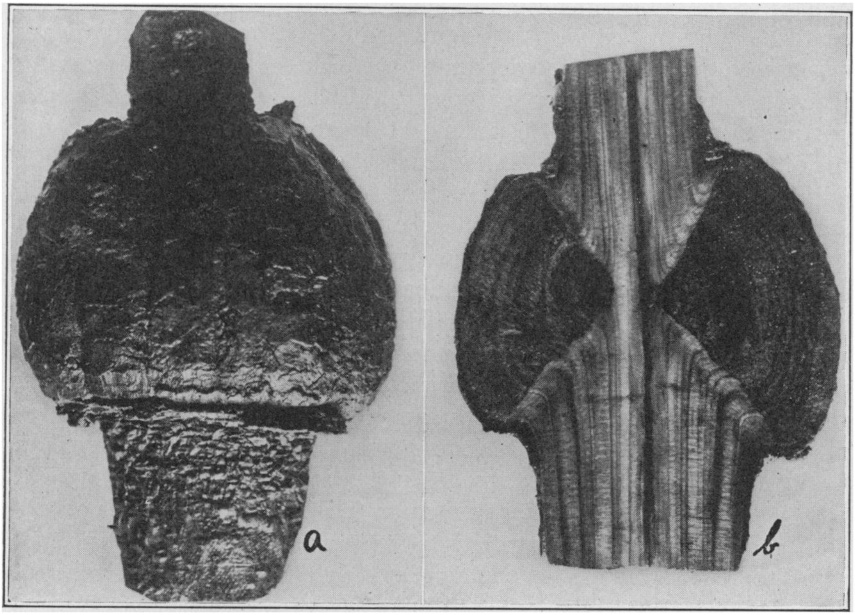
ALBAN STEWART

Peridermium (Aecidium) *cerebrum* Pk. on *Pinus Banksiana* Lamb.

Peridermium cerebrum parasitizes fourteen species of North American pines according to Arthur and Kern (3, pp. 134–135). Owing to the wide range of these species the distribution of the fungus is also wide, occurring nearly throughout the United States, southward to central Mexico, and northward along the mountains to southern Alaska according to the above named authors. The jack pine, *Pinus Banksiana*, is one of the species infected by this parasite, large woody galls resulting on the branches from its attack. A number of these galls came into my possession some time ago, and as a preliminary examination revealed some rather interesting anatomical peculiarities, I thought the material to be worthy of a more careful study. The results of this are given in the following pages.

The galls examined vary considerably in size and age but they all occur on rather young branches. The largest one examined has a cross diameter of 4.7 cm. and the smallest one a similar diameter of about 1 cm. They usually occur singly but two may sometimes be closely associated and later joined together. The outer surface is much roughened due to the scaling off of the outer bark (text-fig. 1*a*), a character which is seemingly more pronounced when spores are being discharged than at other times of the year.

The woody portion of the gall is sharply set off from the normal wood above, below, and inside by the difference in color. The normal wood is light in color, while that of the gall is distinctly brown, probably due to accumulations of resin and other substances in it. This brown coloration is usually more pronounced towards the center, sometimes the outer layers being free from it. In such cases alburnum and duramen portions are well differentiated. Without exception all galls examined show a deep coloration into the first ring of growth at some point or points in the circumference, and tissue abnormalities accompany it. Evidently the fungus was present when this wood was formed and the brown color is not due, at least not entirely, to an infiltration of substances from the layers of wood further out. The galls examined in this respect were of various sizes, some large, others small. More especially were the rather small ones on larger branches examined as these seemed most likely to show an exception if such were true. None of them did, however, so it seems likely that the infection usually if not always takes place during the first year's growth of the branch which bears the gall. This, however, is not true for all species of Peridermium, as Hartig (8, p. 173) describes an instance in which a pine was attacked by *P. Pini* in the fifteenth year of its growth. According to Anderson (2, p. 311) *P. elatinum* seldom attacks branches of *Abies balsamea* over five years old, while *Abies pectinata*, according to de Bary (4, p. 257), is attacked both on young and old parts, and a case is reported where a stem a foot thick and having 60–70 rings of growth was infected.



TEXT-FIGURE 1. Gall of *Peridermium cerebrum* on *Pinus Banksiana*. *a*, external view of the gall, *b*, median longitudinal section of gall. (Both figures about natural size.)

A median longitudinal section through one of the larger galls is shown in text-figure 1*b*. This gall is probably seven years old, as there are that many faintly marked rings of growth in it which correspond with the number of rings in the normal part on the stem just below it. Cross sections of other galls, which were examined microscopically, also show a correspondence in a number of rings both in the gall and in the stem close by. One side of the stem where the gall is located (see text-figure 1*b*) has not as yet become changed at the center, showing that the fungus may spread very slowly in a peripheral direction. The two sides of the stem in this figure show a difference in time of infection, as the wood on the right side near the center is abnormal nearly to the pith, while on the left side there are nearly two rings of normal wood next the pith. The fungus evidently spreads quite as slowly vertically as it does horizontally. The lighter portion in the center of the gall (text-figure 1*b*) is composed almost entirely of normal wood. These zones become broader towards the upper and lower sides so that the gall encloses two more or less cone-like masses of normal wood the apices of which meet near the center. Furthermore it can be seen in this figure that the bark[1] is not appreciably thicker than the bark of the normal stem above and below. The outer portions of this are shed rapidly by the formation of periderm so that nothing remains but the inner phloem and rays. The phloem portion is composed mostly of large cells containing resin and other substances. According to Hartmann (9, p. 32) the bark may become more than three times as thick as normal on branches of the white fir infected with *Peridermium elatinum;* according to de Bary (4, p. 258) however, it may be as much as ten times as thick as normal.

The first striking abnormality to appear in going from the normal wood to that of the gill is a sudden bending outward of the tracheids. The pitting in the walls of these differs rather strikingly from normal in places. According to Penhallow (13, p. 321) the bordered pits in the radial walls of the tracheids in this species of pine are arranged in one row, uniseriate, sometimes in pairs or distinctly two rowed. Specimens of normal wood examined show that the biseriate arrangement rarely occurs. In the wood of the gall the size and arrangement of the pits may differ greatly from normal. The usual arrangement is uniseriate, but two rows of pits often occur and rarely three rows. Where the arrangement is biseriate the pits are usually opposite, but instances are common where there is a strong suggestion of alter-

[1] See Barnes, C. R. "What is Bark?" Bot. Gaz. **22**: 237. 1896.

nate pitting. Illustrating of this tendency appears in plate I, figures 3 and 4, which show about average conditions in this respect. A stronger tendency towards an alternate arrangement occurs sometimes. Rarely both an opposite and an alternate arrangement of pits takes place in the same tracheid wall and occasionally there are transitional stages between these two methods. Where the pits alternate they are sometimes slightly flattened by mutual contact. (See plate I, figure 3). Thomson (16, p. 17) mentions alternate pitting in the cone axis and early wood of the Abietineae and that the pits are sometimes flattened by contact. He also shows on his plate IV, figure 36*c*, a tracheid from the young root wood of *Larix americana* in which there is a suggestion of both opposite and alternate arrangement of pits, a condition which is not strikingly different from what sometimes occurs in the gall under consideration. A slight tendency towards an alternate arrangement of pits is in reality not an uncommon feature in several species of pines. It occurs to a greater or less extent in *P. echinata*, *P. lambertiana*, *P. palustris*, and *P. strobus*. Occurring as it does in several species of pines it is very likely that careful search would reveal it in others. It probably has no great significance in Pinus.

There is a great difference in the size of the pits in the tracheids. They are usually about normal in this respect, but sometimes there are bordered pits present which are very much smaller, often about one fourth the usual size. Large and small pits may occur closely associated in the same tracheid wall. The pits may be scattered or closely arranged (figure 4).

According to Gerry (6, p. 122) the pines and other conifers with abietineous affinities always have bars of Sanio present in the walls of the tracheids, while in the Araucarineae they never occur. Jeffrey (10, 544–545), however, has subsequently found them to be present in certain regions of *Araucaria Bidwellii* and *A. imbricata*. By staining with Haidenhain's haematoxylin and safranin according to the method described by Jeffrey (l.c., p. 547), these bars can be easily seen in some of the tracheids of the gall but they fail to appear in others. They may stand out sharply in one while in another adjacent tracheid they can not be seen, or, they may appear in one part of the wall and not in another. Very faint traces of them occur at times. As so much depends on the methods of staining in order to see these bars, it is hardly safe to say positively that they are absent at times from the tracheids of this gall. If they are invariably present I have not always been able to see them. They are probably sometimes absent. Thomson (16, p. 22, pl. 4, fig. 36*a*) has found a somewhat similar condition, as he states that "where the pits are multiseriate, as in young root wood, '*Larix americana*' there may not be a trace of the bar of Sanio."

The walls vary in thickness, individual tracheids showing differences in this respect. This condition is very noticeable in longitudinal sections, but it is less marked in cross sections (see plate I, figure 1). The walls are often sinuous (figure 4), causing wide and narrow places in the same tracheid. Where this condition is pronounced inflations in the walls may result from it. Blunt end walls are common. The length of the tracheids varies greatly and as a whole they are shorter than in normal wood. Cells which are isodiametric or nearly so occur commonly, which show their tracheary character in the pitting. Wörnle (18, p. 132) has described similar cells near the broad rays in juniper stems infected with *Gymnosporangium uniperinum.* The formation of these short tracheids possibly comes about by the cross division of cambium daughter cells. Such is the case in traumatic wood according to de Vries (5, p. 21).

Cells occasionally occur which have the character of both tracheids and parenchyma cells as the pits in one part of the wall are bordered and in another part plain. The plain pits occur in such places as to leave no doubt about their true character. They were not mistaken for one-sided bordered pits as they do not occur in opposite rays. Mäule (11, p. 5, plate II, figure 1) describes and figures cells somewhat similar to these in the traumatic wood of *Abies cephalonica,* Thompson (15, p. 336) describes transitional cells which are normally present in the rays of *Abies homolepis,* and Groom and Rushton (7, p. 474, figure 16) mention simple pit-like structures between the bordered pits in *Pinus excelsa,* a species from the Himalayas. True wood parenchyma cells also occur in this gall, which have nuclei and other protoplasmic contents. Such cells do not occur normally in the pines according to Penhallow (13, p. 112). They appear to be more numerous among the tracheids which first bend outward from the normal wood into that of the gall, but this may be due to the fact that there is less resin in these parts so that they can be more readily seen there, and their true character recognized, than deeper in the gall.

Cross sections cut through the center of the gall usually show that the arrangement of the tracheids is not strikingly different from normal (see plate I, figure 1). Disturbance in the arrangement does occur sometimes in which the tracheids are usually turned over to right and left tangentially, probably indicating regions of ball-formation of tracheids. Similar conditions occur in juniper stems infected with *Gymnosporangium juniperinum* according to Wörnle (18, p. 83). The width of luminae and thickness of the walls of the tracheids does not differ greatly from that of normal cross sections except in the summer wood where the walls are much thinner than in normal summer wood (see plate I, figure 1). This is quite different from the wood of *Abies balsamea* infected with *Peridermium elatinum*, as Anderson (2, p. 337) has reported thicker walled tracheids than normal. There are but few layers of summer tracheids formed, and it is due to this fact that the rings of growth are sometimes not well defined. A similar condition may result in juniper stems infected with *Gymnosporangium juniperinum* according to Wörnle (l.c.). If cross sections are cut above or below the center of the gall they will usually show a structure between cross and tangential. This peculiar condition is due to the fact that the tracheids pursue a more or less horizontal course for some distance after they bend outward into the gall from the normal wood.

In radial sections the course of the tracheids follows in a general way the outer contour of the gall (text-figure 1*b*). There are some exceptions, however, as a nearly true transverse structure may occur as well as wavy structure. In tangential sections the normal course of the tracheids is often very much disturbed, resulting in wavy structure and balled or whorled arrangement. Large whorls, very complex in structure, sometimes occur in such sections (plate I, figure 2). According to Mäule (11, p. 10) these seldom appear in other than tangential sections of traumatic wood. I have found this to be true in this gall and in the gall of *Andricus punctatus* on the black oak, see Stewart (17, p. 541). Small tracheid whorls occur in traumatic wood of the jack pine but I have failed so far to find any which approach in any way the size of the one shown in figure 2. Large structures of this kind do sometimes occur in traumatic pine wood, however, as Mäule (l.c., p. 12) reports them from *Pinus Pumilio*. U- and Y-shaped tracheids are common in regions of extreme distortion in the gall.

In addition to the fusiform rays, which are low and scattered in the normal wood, three sorts of rays occur in the wood of the jack pine. According to Penhallow (13, p. 321) there are: "(1) low rays composed of oblong narrowly oval thin-walled parenchyma cells with narrowly oblong, terminal tracheids; (2) low rays of similar composition, but the parenchyma cells much thinner walled; (3) the highest rays composed chiefly of narrow tracheids with a few broader, oblong parenchyma cells interspersed." I have found it difficult to distinguish between groups 1 and 2, but the rays of group 3 are readily distinguished, and from the single specimen examined, I find that they are in general 6–10 cells high. Both low and high rays can be seen in tangential sections of the gall, the higher ones being the more common. These usually do not exceed the normal rays of group 3 in number of cells in height, but where exceptions occur the increase is largely due to the addition of more rows of parenchyma cells. The individual cells composing the rays are usually larger than normal.

With the exception of fusiform rays, Penhallow (13, p. 94) states that the rays are always uniseriate in Abies, Picea, and Pinus. It is a common thing to find rays in tangential sections of this gall which are two cells wide in part (plate I, figure 5) and occasionally a ray which is three cells wide. It is evident that these are not fusiform rays, which occur more abundantly in the gall than in normal wood, as they do not partake of the character of such rays. A similar condition of ray structure also occurs in traumatic wood of this species of pine (plate I, figure 6).

A sporadic tendency to a slight broadening of the rays occurs in a few of the living conifers according to Penhallow (13, p. 94). It may be met with in species of Pseudotsuga, Cupressus, Juniperus, Sequoia, Araucaria, and Larix. In Libocedrus the tendency is more pronounced. A significant broadening of the rays may take place according to Mäule (11, pl. 2, figure 8), in traumatic wood of *Abies cephalonica*, a genus in which such does not occur normally. Wörnle (18, p. 131, figure 8) has also recorded a marked broadening of the rays in stems of Juniperus infected with *Gymnosporangium juniperinum*, ray-like structures figured by this author being nearly as broad tangentially as they are high in some instances.

Certain authors have recently given a phylogenetic significance to the broadening of the rays in traumatic wood of some of the angiosperms. I believe that it is pretty generally accepted that the uniseriate ray is primitive in the Coniferae. If this conception is correct the broadening of the rays in its members, due to traumatic and other stimuli, can not be considered of phylogenetic importance. They may be formed to supply some need of the plant, and if such is true they are probably physiological rather than phylogenetic in their significance. Taken as a whole we know comparatively little about the structure of pathological plant tissue, and until more is known it is hardly safe to base any very strong conclusions on it phylogenetically.

The rays are more numerous in the gall than in normal wood, a given area of tangential section of the gall having approximately twice as many rays present as the same area of normal wood. The proportion of ray tissue is greater than this, as the cells are larger as a rule and more numerous in the rays of the gall. It might be well to mention in this connection that Anderson (2, p. 337) found that there were often twice as many rays present in parts of *Abies balsamea* infected with *Peridermium elatinum* as there were in normal parts.

The ray tracheids present some interesting peculiarities. In the normal wood of the jack pine these are strongly reticulated, in the gall the reticulations are often very much reduced or absent entirely. The ray tracheids thus combine characters of both hard and soft pines. Tracheids sometimes border the rays (center of plate I, figure 4) which are similar in many respects to the peculiar tracheids figured by Thompson (14) from the rays of the traumatic stem wood, and the normal root wood of *Pinus resinosa.*

Resin canals are few and widely scattered in the older wood of the jack pine but are more numerous in the younger wood near the pith. Close associations of canals occur but seldom in either the young or old wood. In cross sections of galls the canals may be as much as three times as numerous as in the normal wood, varying somewhat in different individuals. They are often arranged in concentric rings, so closely associated in places that only the rays intervene (plate I, figure 1). Anderson (1, p. 472) found a similar arrangement in parts of Abies infected with *Peridermium elatinum.* The canals in this gall have a lining of living nucleated cells and are evidently not merely resin passages such as are described by Mäule (11, p. 18) from the traumatic wood of certain conifers. A great increase over the normal number of resin canals sometimes takes place in traumatic pine wood. According to Thomson (16, p. 38) there may be 7–8 times as many as normal in the traumatic wood of *Pinus resinosa.*

An interesting thing in connection with the distribution of resin canals in this gall is the fact that there is no increase in the number in the uninfected parts above the gall. Anderson (1, p. 473) states that the parts of *Pinus Strobus* above infections of *Agaricus meleus* contain more resin canals than do normal branches. He also reports the presence of resin canals in the branches of Abies which are above infections of *Peridermium elatinum*. A similar condition is mentioned by Mer (12, p. 367) in Abies, above infections of *Phoma abietinae*.

We have in this instance a rather striking correlation between the effects produced by two species of the same fungus. In one case the fungus is unable to exert an influence on the structure of the host beyond where it is actually present in the tissues of the same, in the other case it is far reaching in its effects, and is not only able to modify the tissue of the host some distance from the parts infected, but is also able to stimulate the productions of organs that are not normally present there.

SUMMARY

The more important facts presented in this article are briefly summarized below:

1. Both an alternate and an opposite arrangement of bordered pits in the radial walls of the tracheids.
2. An unequal thickening of the walls and luminae of the tracheids.
3. Very short tracheids with blunt end walls, which resemble parenchyma cells except in the pitting.
4. Cells which are transitional between tracheids and parenchyma cells in the pitting.
5. The presence of true wood parenchyma cells.
6. A small production of thin-walled summer tracheids.
7. A probable absence of bars of Sanio from many of the tracheids.
8. An increase in the number of rays in the gall wood.
9. A tendency towards the production of multiseriate rays.
10. Ray tracheids which are transitional between those of both hard and soft pines.
11. The presence of a balled or whorled arrangement of tracheids in tangential section.
12. A great increase in the number of resin canals in the gall wood but no such increase in the uninfected wood close by. The examination of this gall has revealed so many points of anatomical interest that a further study of this subject seems to be worth while.

On this account the author expects from time to time to issue other papers on the anatomy of Peridermium galls on pines and other conifers.

METHODS

In preparing material for sectioning it was first treated with strong hydrofluoric acid for several weeks to soften the tissue. The sections were stained with Heidenhain's haematoxylin and safranin by the usual methods employed in staining wood sections.

DEPARTMENT OF BOTANY,
UNIVERSITY OF WISCONSIN, MADISON.

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EXPLANATION OF PLATE I

All figures are from the jack pine, *Pinus Banksiana.*

FIG. 1. Cross section through a portion of a gall showing abnormally produced resin canals and thin-walled summer tracheids. × 65.

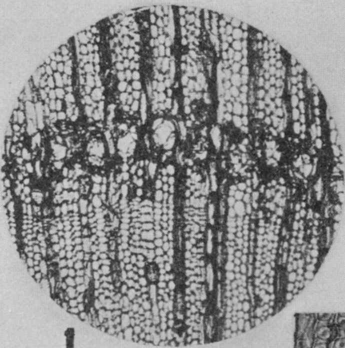
FIG. 2. Tracheid whorl or "ball-formation" from tangential section of gall. × 65.

FIG. 3. Portion of a radial section through gall showing alternate arrangement of pits. × 125.

FIG. 4. Portion of a radial section through gall showing irregularities in walls of tracheids, peculiar ray tracheids, and alternate pitting. × 125.

FIG. 5. Portion of a tangential section through gall showing a tendency towards a broadening of the rays. × 125.

FIG. 6. Tangential section of traumatic wood. × 65.



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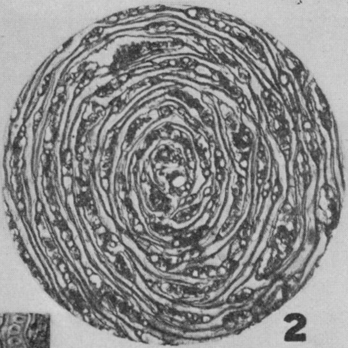

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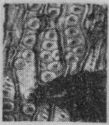

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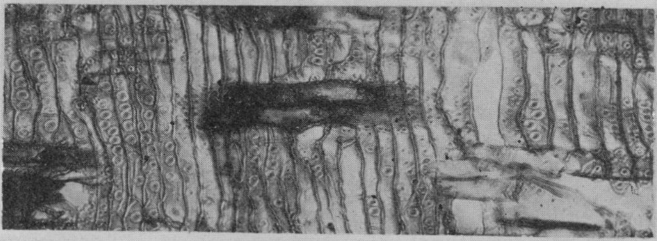

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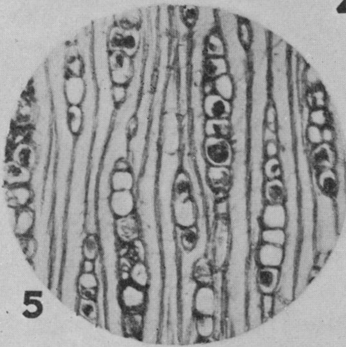

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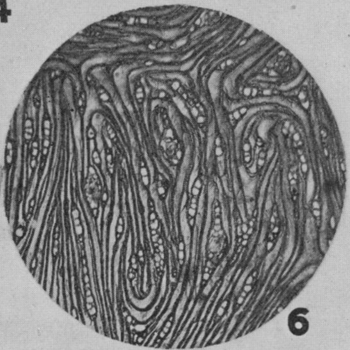

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STEWART: ANATOMY OF PERIDERMIUM GALLS.